GROWTH IN TREES.[1]

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(PLATE I.)

My studies of the course and physical conditions of growth were extended to include the changes in circumference and diameter of tree trunks as well as the elongation of growing branches in 1918, and a new technique with specially designed instruments was found necessary for the analytical study of the changes in volume of these massive organs. The records are now continuous for a large number of trees for many months, one tree having been under continuous measurement since September, 1919.[2]

Two new instruments were designed for obtaining measurements of growing trees. The dendrograph, an instrument for making continuous records of the variation of tree trunks, is an instrument consisting of a floating frame of metal of low temperature coefficient, such as invar or bario, which may be placed around a tree trunk, and the variation in distance between a contact rod on one side of the trunk and of one end of a rod or lever on the other side is traced by a pen on the free end of a lever on a sheet of paper carried by a recording cylinder. Such measurements are in terms of the diameter. In an earlier form of the instrument two levers were employed. One end of a bearing lever was placed in contact with the tree, the free end being linked to the short arm of the recording lever. The results previous to October, 1920, were obtained by

[1] The full paper of which this is a synopsis will be published by the Carnegie Institution of Washington as prospective No. — of its series.

[2] MacDougal, D. T., "The Dendrograph; a New Instrument for Recording Growth and Other Variations in the Dimensions of Trees," Carnegie Inst. Wash. Year Book for 1918, pp. 59–60. "The Dendograph," *ibid.*, for 1919, pp. 72–78. "The Coure of Growth in Trees as Measured by the Dendrograph," *ibid.*, for 1920, pp. 51–52. "Measurement of a Season's Growth of Trees by the Newly Designed Dendrometer," *ibid.*, for 1920, p. 52.

this type of instrument. The older and the improved lever sets are illustrated in Plate I, Figs. 1 and 2.

A dendrometer of simple design has been perfected which may be placed around the trunk of a tree and the size of the trunk read on a dial from time to time. The essential parts of this instrument are an encircling wire engaged with a number of bearing levers. One end of the wire is anchored and the other is attached to the short end of a lever, the free end of which moves over a scale giving readings of the size of the trunk in terms of several radii, or of the circumference.

By the assistance of collaborators measurements of a number of evergreen and deciduous trees in various habitats from the Atlantic seaboard to the Pacific coast were made in 1919 and 1920. Beech, ash, walnut, sycamore, pines, spruce, fir, poplar and oak trees were included in the list.

The principal generalizations supported by the information obtained may be briefly summarized as follows:

The period in which enlargement of trunks takes place is comparatively brief even in places in which the season is of indeterminate duration. Growth is an activity of an embryogenic tract of tissue, the activity of which depends upon environmental conditions, and no part of the observations suggested a seasonal rhythmic action. The Chihuahua pine which exhibits growth of the trunk with that of the branches on the dry mountain slopes with the advance of the temperatures in May and June, is brought to rest coincident with the desiccation of the soil in the dry fore-summer. Reawakening ensues consequent upon the summer rains and enlargement continues until checked by the decreasing temperatures and increased soil desiccation in the autumn.

The Monterey pine (*Pinus radiata*) shows beginning growth of the trunks with the advance of temperatures January to April, and comes to rest in July with the desiccation of the soil. *Quercus agrifolia* in the same region begins earlier and ceases to grow in June or July. Both may be awakened in July or August by deep irrigation of the soil (Fig. 3).

The trunks of all the trees measured show a daily variation in size, by which the maximum is reached shortly after sunrise and the minimum at a time after noon, dependent upon external agencies. These variations appear to depend upon the water-balance in the woody cylinder, are greatest in the seasons in which water-loss

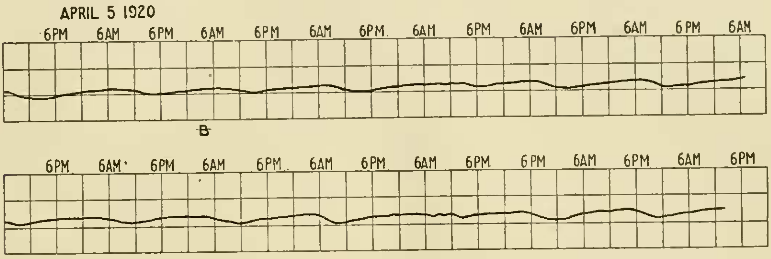

FIG. 3. *A,* dendrographic record of variations in diameter of Monterey pine tree 1 meter from the ground for week beginning April 5, 1920. *B,* record from instrument attached to the trunk 9 meters from the ground. Daily equalizing variations with actual enlargement beginning mid-week × 8, on a scale of 10 mm. intervals.

from the crown is greatest, are least in the cooler or damper seasons, and are to be detected in the records even in the period of most rapid enlargement of the trunk (Fig. 4).

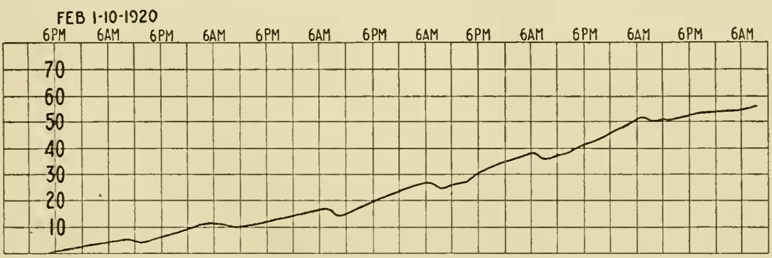

FIG. 4. Auxographic record of elongation of terminal internode of young pine tree showing cessation of growth and shrinkage during the mid-day period, coincident with the decrease in diameter of trunks of larger trees, × 3, on a scale of 10 mm. intervals.

The trunk of a tree may in fact be compared to the supply hose of a fire engine coupled to a hydrant. When the pressure from the mains is enough to supply water faster than it can be pumped out the hose is distended. When the engine tends to take water faster than it would be delivered by the system, the hose would tend to collapse. Something of this sort takes place in many trees which have been kept under observation. The conduit in this case however is not a simple pipe or a set of pipes, but is made up of vessels through which water may pass under capillary conditions, and enclosed box-like tracheids which may be only partially filled with water. When water is withdrawn from such a system faster than it is taken in the resulting changes in form and size are complex in character, but are expressed by the well-defined daily equalizing variations which are of a characteristic type for each kind of tree (Fig. 5).

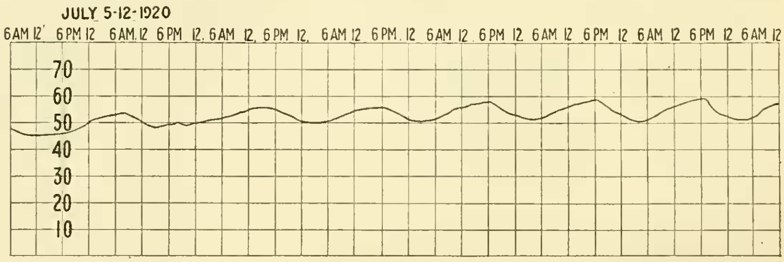

Fig. 5. Dendrographic record of Arizona ash near the end of the growing season. The daily equalizing variation is large, but the diameter shows an increase on each successive day. Variations × 10 on a scale of 10 mm. intervals.

The greatest daily equalizing variations were shown by Fraxinus, Pinus, Picea, Pseudotsuga and Juglans, and lesser variations were displayed by Populus, Platanus, Fagus, Quercus and Citrus. No available facts furnish the basis of an adequate explanation of such differences.

Estimates of the range of daily equalizing variations in a Monterey pine taken from bearings on a thin layer of cork external to the bast of a trunk which had ceased to grow for the season shows that the diameter might vary one part in 1,750. That a large share of this variation is due to changes in the hydration of the living cells is proved by the fact that when bearings are taken on the woody cylinder of the trunk internal to the growing layer the variation drops to one part in 8,750 of the diameter. The actual change in volume in the first instance calculated on the basis of a conical trunk 18 meters high and 35 cm. in diameter at the base would amount to about 400 cu. cm. of which not more than one-fifth or 80 cu. cm. is attributable to variations in the wood. It is to be noted however that the change in the volume of the wood may by no means be taken to represent the water deficit in the wood. The woody mass is made up of box-like cells, which may include a bubble of gas, the water forming no more than a thin film on the wall of the cell and enclosing the gas bubble in the condition of extreme water deficit. The withdrawal of water through the walls of the cells which are semi-rigid, increases the surface tension of the gas bubble, which results in a slight lessening of volume of the whole mass, but in an amount that would constitute no more than a small fraction of the total of the water loss.

Awakening and growth of the terminal buds with resultant elongation of leaders and branches generally begins some time before enlargement of the trunk takes place in many trees. The period separating the two may be no more than a week in *Quercus agrifolia* and has been seen to be as much as ten or twelve weeks in *Pinus radiata*. Observations on the Parry spruce and Douglas fir show that the trunks of these trees are enlarging at a time when the buds are in a very early stage of enlargement.

In the single case in which dendrographs were attached to a pine tree 1 meter and 8 meters above the ground growth began coincidently at the two places in 1920. In the following year, however, the dendrograph at the higher point on the trunk recorded enlargement a few days before any action near the ground was made visible. In February, 1921, an auxograph was brought into bearing on the internode of a pine tree five or six years old which had been formed in 1919. The buds had made a growth of 4 or 5 cm. but no action had yet begun in the internode. A second instrument was brought into bearing on the middle of the internode formed in 1920 on another young tree. Steady enlargement was in progress.

The embryonic layer of a tree is in the form of an enclosing sheath terminating in the cones of the growing points. Activation of this tract is generally initiated in the growing points. Swelling in the cambium layer may be practically coincident with this awakening in some trees. Cases are recorded in the following paper in which weeks elapsed between the awakening of the buds and the enlargement of the base of the trunk. Activation of the growing cells may be taken to depend upon the localized food-supply, temperature, moisture or other factors.

The fact that growth depends upon physical conditions largely external instead of being a manifestation of a rhythm on the part of the tree is well evidenced by tests in which trees which had ceased to grow with the seasonal drying out of the soil were awakened by a renewed water supply.

Irrigation of the soil which had a moisture content of less than 6 per cent. around the roots of a Monterey pine was followed by progressive enlargement constituting growth at the base of the tree, and at a point 8 meters higher within 24 hours. The distance from the absorbing surfaces of the roots through which the added water supply must enter could not be less than 3 meters from the lower instrument and the influence of the added supply was felt at the upper instrument 11 meters from the absorbing surfaces within the day. It does not seem possible that water could have been conducted through the tracheids this distance within the given length of time.

An irrigation test similar to the above was made with a small California live oak (*Quercus agrifolia*). The results were even more startling than those described for the pine. Within two hours the dendrograph which had its contacts with the tree at least 3 meters from the absorbing surfaces showed some enlargement, an action which may be directly connected with the fact that the vessels in this oak are numerous and large.

The irrigation experiments might be held to simulate the effects of stream overflow, which if due to melting snows would not be accompanied by any marked higher humidity. It is seen to result in the formation of a tapering shell of wood which was as thick as the seasonal formation at the base of the trunk, but which had but half this thickness 8 meters higher up on the trunk. The layer of normal formation was of practically identical thickness at the two places.

One of the earliest series of measurements which would enable the forester to follow the seasonal variations of trunks was that made by C. E. Hall at San Jorge, Uruguay, in 1885–1890, by commonly used methods of calibration.[3] Friedrich perfected a device for

[3] Hall, C. E., "Notes on Tree Measurements Made Monthly at San

automatic registration of changes in circumference taken up by a steel band in 1905,[4] but I have been unable to find any description of results obtained. Such results would include the errors due to the high temperature coefficient of steel. Some measurements of expansions of trunks as solid columns were made by Trowbridge and Weil in 1918,[5] but the most serious effort with accurate methods was that of Mallock in 1918, who used an arrangement including a tape of invar passed around the trunk and two superposed plates of glass by which changes in circumference caused displacements in interference bands of light. Direct and continuous observation yielded accurate results of value with regard to daily equalizing variations as well as of actual growth.[6]

The trunk of a tree is largely composed of dead cells, but enclosing it is a thin sheet of spindle form cambium cells[7] in 2 to 10 or more layers which in the growing season enlarge in thickness and divide lengthwise, those on the outside becoming transformed into phloem cells and those on the inner into wood cells or tracheids. Extending from the center of the trunk are thin sheets or rays of the medulla or pith of the young stem. The most recently formed cells of these elements are still living and in some trees the medullary cells remain alive for several years, so that the woody cylinder of the tree may comprise wood-cells or tracheids, vessels and thin-wall ray cells, some of which are alive. Externally to the cambium are sieve cells, bast fibers, etc., and cork cells, enclosed in a bark which varies widely as to structure in different species.

The greatest amount of increase or change in volume is that which results from the multiplication by fission of the cambium elements, and the following enlargement of the derivatives. The facts

Jorge, Uruguay, from Jan. 12, 1885, to Jan. 12, 1890," *Trans. Bot. Soc. Edinburg*, 18: 456, 1891.

[4] Friedrich, J., "Zuwachsautograph," *Centralb. für das gasammte Forstwasen*, 31. Nov., 1905, pp. 456–461.

[5] Trowbridge and Weil, "The Coefficient of Expansion of Living Tree Trunks," *Science*, 48: 348, 350, 1918.

[6] Malloch, A., "Growth of Trees with a Note on Interference Bands Formed by Rays at Small Angles," *Proc. Roy. Soc.*, 90, B, 186–191, 1918. Submitted Dec. 1, 1917.

[7] Bailey, I. W., "Phenomena of Cell-division in the Cambium of Arborescent Gymnosperms and their Cytological Significance," *Proc. Nat. Acad. Sc.*, 5: 283–285, 1919.

are not yet available for a definite determination of the part which growth in the phloem may play in the variations as recorded by the dendrograph. Much however is known as to the cytological program of the growing elements in cambium and phloem. A correlation of facts of this kind and of the seasonal changes in food supply will be necessary to interpret the "growth-impulses" lasting for a few days late in the season, displayed by many trees.[8]

Dendrographic data, especially records of experimental settings, may be expected to afford further necessary corrections as to the time element in the interpretation of seasonal layers or "annual rings" upon which much reliance is placed as offering corroborative evidence as to climatic periods and solar cycles.

Illustrations.

Plate I.

Fig. 1. Earlier form of dendrograph which takes a bearing from a prepared area on the bark of the tree by one end of a small lever, the other end of which is connected with the short arm of a recording lever. An encircling belt of wooden blocks serves as a base and support. Flexible wire standards with a base of thin sheet metal are clamped in position on the wooden blocks and screw clamps which slide up and down on the wire standards serve to hold the floating frame in a horizontal position. The entire apparatus is so adjusted that a contact rod of the floating frame on the opposite side of the tree is held with gentle pressure against the tree and any variation in diameter is then expressed by movements in the lever set.

Fig. 2. Improved dendrograph lever set. *A,* inner end of quartz rod in contact with prepared surface on the bark of the tree. The outer end of the quartz rod is fitted with a metal guide which engages the short arm of the recording lever at *B*. The long arm of the recording lever *D* carries a pen which makes a tracing on ruled paper on a revolving drum. The horizontal member of the frame *C* which carries the recording lever may be toward or away from the tree to adjust the pen at any point on the paper record sheet.

[8] Knudson, L., "Observations on the Inception, Season and Duration of Cambium Development in the American Larch (*Larix laricina* Du Roi Koch)," *Bull. Torr. Bot. Club,* 40: 271–293, June, 1913.

Brown, H. P., "Growth Studies in Forest Trees. I. *Pinus rigida* Mill.," *Bot. Gaz.,* 54: 386–402, 1912. "II. *Pinus strobus* L.," *ibid.,* 59: 198–240, 1915.

Bailey, I. W., "Phenomena of Cell-division in the Cambium of Arborescent Gymnosperms and their Cytological Significance," *Proc. Nat. Acad. Sci.,* 5: 283–285, 1919. "The Cambium and Its Derivative Tissues. II. Size variations of Cambium Initials in Gymnosperms and Angiosperms," *Amer. Jour. Bot.,* 7: 355–367, 1920. "II. A Reconnaissance of Cytological Phenomena," *Amer. Jour. Bot.,* 7: 417–434, 1920.